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FORUM PAPER

What is an alliance?

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Abstract

The alliance is the basic unit of the EuroVegChecklist, and it often serves as the lowest rank in broad-scale vegetation surveys. However, there is hardly any literature about the concept and definition of this syntaxonomic rank, leading to uncertainty in its application. Here, I explore the original association concept of Braun-Blanquet, which was based on absolute character species, and I show that this concept is more or less identical with the units that we now call alliances. By also incorporating the concept of central syntaxa, I propose the following definition: "An alliance is a moderately broad vegetation unit that either has one or several absolute character taxa or that can be interpreted as the central alliance of an order." The one-to-one relationship between character taxa and vegetation units gives the latter a clear biogeographical and evolutionary meaning. Restrictions to the validity of character taxa – either to certain geographical areas or to physiognomic types – cause theoretical and practical problems and should be avoided. Possible exceptions are species with similar frequency in two formations or species introduced to other continents.

Taxonomic reference: Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/) [accessed 1 July 2020].

Keywords

Alliance, Braun-Blanquet approach, character species, EuroVegChecklist, phytosociology, syntaxonomy, vegetation classification

Introduction

The alliance is the basic unit of the EuroVegChecklist (EVC; Mucina et al. 2016), and it is frequently used as the smallest unit in supra-regional phytosociological revisions (e.g., Čarni et al. 2009; Peterka et al. 2017). However, there is very little literature about the concept and definition of this syntaxonomic rank.

The alliance (in German: Verband) was introduced by Braun-Blanquet (1921) as a synonym to "association group" (Assoziationsgruppe), meaning a group of floristically related associations. The effective start of the alliance concept was 1926, when several important monographs were published (and many of those alliance names are still in use) (Braun-Blanquet 1926; Braun-Blanquet and Jenny 1926; Koch 1926; Luquet 1926). None of those monographs, or subsequent works provided an explicit definition for the units above the rank of association, but the general agreement was that an alliance should have supra-regional character species that are shared by some or all of its associations. Textbooks of phytosociology (e.g., Pavillard 1935; Braun-Blanquet 1964; Westhoff and van der Maarel 1978) did not much elaborate on the topic. Unlike the association concept, which has been the subject of heated debates in the phytosociological literature (Dengler 2003; Willner 2006; Guarino et al. 2018), the evolution of the alliances was much smoother, although their number has steadily grown over the last century. In recent years, the alliance has also been adopted in classification systems not using the traditional Braun-Blanquet approach (Jennings et al. 2009; Faber-Langendoen et al. 2014).

In the absence of a commonly agreed definition for the alliance (at least in Europe), recent decades have witnessed an increasing tendency of splitting long-established alli-

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ances and describing new ones lacking supra-regional or absolute character species. The EuroVegChecklist (Mucina et al. 2016) lists 1108 alliances (excluding those of vegetation dominated by non-vascular plants), which is an increase of ca. 20% compared to the overview of Rodwell et al. (2002). To enable the evaluation of all proposed alliances, we need objective criteria. Therefore, I propose to revisit Braun-Blanquet's original association concept and transform it into a definition of the alliance which is both operational and theoretically founded.

Braun-Blanquet's original association concept – more like the modern alliances

After preliminary considerations on the subject (Braun 1913; Braun and Furrer 1913), Braun-Blanquet presented a first, fully developed association concept in his thesis (Braun 1915). Based on the definition given by Flahault and Schröter (1910), he emphasised that the association is primarily a floristic unit. He then identified three components of the floristic composition of a vegetation unit: dominant, constant and characteristic species. The third category (called "character species" hereafter) was defined as those species which were either restricted to a certain association (character species of first order) or had at least their optimum therein (character species of second order). Braun-Blanquet argued that the character species should have the highest weight in the delimitation of the associations, as they represented the ecology and evolution of the vegetation unit better than the dominant and constant species. Thus, he defined the association as "a vegetation unit of definite floristic composition which, by the presence of character species, exhibits an ecological independence" (translated from French and German).

The only higher rank used by Braun (1915) was the "association group" ("groupe d'associations"). Like the association, the association group had its own character species, i.e. species with broader ecological amplitude, common to several or all associations of the group while being rare or absent outside the group. Braun-Blanquet argued that, unlike the formations, which are defined by physiognomic criteria, vegetation units defined by character species contain not only ecological but also biogeographical and evolutionary information.

Despite the fact that the "association group" was synonymised with the alliance in Braun-Blanquet (1921), the groups of Braun (1915) basically correspond to classes in the modern phytosociological system. The associations, on the other hand, are more or less identical to units that we now call alliances (see Suppl. material 1). This was not because most alliances were represented by only one association in his study area (the Cévennes in southern France). Instead the extensive discussion of the variability and distribution of each association proves that Braun (1915) indeed perceived the associations as much broader units than in his later works. For example, under the "Association à *Potentilla caulescens* et *Saxifraga cebennensis*", he wrote (translated from French): "The Pyrenees on one side and the Alps on the other, present not only races but also different altitudinal forms." About the "Association du hêtre", he noted: "Wherever we encountered beech forests, from the Baltic Sea to the Alps and the Pyrenees, nearly the same phanerogamous species formed the understorey. We can hardly recognize them as distinct regional variants. […] The distinction of two main races of the association seems possible today, however. Several beech companions have a clearly southern distribution and do not exceed north of the latitude of Paris and Central Germany. […] The variant of northern Europe contrasts with the southern race by its poverty in special elements."

Braun-Blanquet's second association concept

The original definition of character species did not include any geographical restriction. Indeed, the whole idea of associations as biogeographical-evolutionary units relies on the one-to-one relationship between the species and the vegetation unit. However, while being a brilliant theoretical concept, the associations defined in this way turned out to be too broad for detailed vegetation studies. In the years following Braun-Blanquet's thesis, the original association concept was gradually and almost surreptitiously transformed by using "regional character species" instead of absolute ones. The new concept was made official in a footnote in volume 5 of the "Prodrome of plant communities" (Braun-Blanquet and Moor 1938): "In the progress of phytosociological studies it has become evident that the associations are individualised by regional and even more or less local character species rather than by absolute ones. The character species of the alliances and orders, in contrast, have a much more general validity. They only occur in other alliances and orders in a constitutive manner if they are distributed over two or more big circles of vegetation (eurosiberian circle, mediterranean circle etc.)" (translated from German).

Therefore, for the purpose of the association concept, the validity of character species was restricted to "floristically homogenous regions", often not larger than a particular valley in the Alps. This allowed Braun-Blanquet to maintain his original definition of the association, which requires at least one character species for each association, while in fact they were only defined by differential species. The concept is best illustrated in Braun-Blanquet's monograph of the inner-alpine dry valleys (Braun-Blanquet 1961), where the vicariant associations of an alliance mostly have the same regional character species that are in fact character species of the alliance. Thus, the new associations were basically geographical subdivisions of the alliance, whereas the old associations became the alliances. This concept worked surprisingly well, despite

the fact that nobody could give a clear definition of a "floristically homogenous region" (Willner 2006), and the original association concept was forgotten.

Back to the roots: towards an operational definition of the alliance

According to Braun-Blanquet, the character species of alliances have a much more general validity than those of the association, being geographically constrained only by the "circle of vegetation." The latter, however, remained an elusive concept that has not been used in the phytosociological literature for many decades. In fact, geographical restrictions to the validity of character species are very problematic for both practical and theoretical reasons. On the one hand, any delimitation of areas of validity is arbitrary, circular or based on external criteria not derived from the vegetation itself. On the other hand, the one-to-one relationship between taxa and vegetation units is destroyed, thus weakening the biogeographical and evolutionary significance of the syntaxonomic system. I therefore suggest that we abandon all geographical restrictions and only use absolute character taxa for higher syntaxa. The term "*character taxa*" underlines the fact that subspecies may be used to define higher syntaxa as long as they are really genetically different. In certain cases, the use of supraspecific taxa might also be reasonable, e.g. in vegetation types characterised by closely related species with narrow geographical ranges (Deil 1994).

An "*absolute character taxon*" is a taxon which has its global optimum in the syntaxon in question. Obviously, a taxon can only be an absolute character taxon of exactly one syntaxon. Possible exceptions could be cryptic taxa (i.e., morphologically indistinguishable, but genetically isolated infraspecific entities), and species introduced to other continents and genetically differentiated from their native range (e.g. *Robinia pseudoacacia* in Europe; Bouteiller et al. 2019). Such cases could be seen as "subspecies in statu nascendi" and used as character taxa of higher syntaxa, provided that the latter are sufficiently different in their overall species composition. In contrast, geographically isolated ranges without accompanying genetic differentiation would not be sufficient to use a character taxon for two different syntaxa.

Building upon these ideas, and incorporating the concept of central syntaxa (see below), I propose the following definition:

"An alliance is a moderately broad vegetation unit that either has one or several absolute character taxa or that can be interpreted as the central alliance of an order."

There are several aspects in this definition that need further explanation. The term "*moderately broad vegetation unit*" refers to the relative position of the alliance in the syntaxonomic hierarchy, being intermediate between the more narrowly defined association and the broader units above. Indeed, analogous definitions should be adopted for the order and class level, the latter being broad and very broad vegetation units, respectively, though physiognomic considerations might come into play at these ranks as well (see below). A more precise specification of the range of compositional variability covered by an alliance seems hardly possible and even undesirable given the extreme differences among different types of vegetation.

A "*central syntaxon*" is a syntaxon which has the diagnostic species of the next higher unit but is only negatively differentiated from the next similar units of the same rank. Per definition, there can be only one central syntaxon within each higher unit. The concept was introduced by Dierschke (1981) for associations bearing the character species of the alliance, but lacking character species of their own. Later, Dengler et al. (2005) argued that the same logic can be applied to higher syntaxa. Indeed, many alliances adopted in the literature are central syntaxa, although this fact is often obscured by the enumeration of "regional character species." A prominent example is the *Galio odorati-Fagion* (Central European basiphytic beech forests) which is only negatively differentiated from their counterparts in southern Europe (Willner et al. 2017). It contains most of the character species of the order *Fagetalia sylvaticae* but has no character species of its own. A potential argument against central alliances could be that in this way the delimitation of the alliances becomes dependent on the orders, and therefore the system would have to be developed top-down instead of bottom-up. However, in reality, syntaxonomy is always a combination of top-down and bottom-up perspectives. Regional and national monographs often disagree on the syntaxonomic rank at which a species is characteristic (e.g., the same species is considered as characters species for an alliance in one study and for the whole order in another study). The appropriate rank for each species can only be determined by a broad-scale comparison. Thus, an alliance previously considered to have several character species of its own might turn out to be the central alliance of the order. However, as there can be only one central alliance per order, it could also mean that several alliances must be merged. The same logic applies to the orders within a class.

It is now widely recognised that floristically defined units should be constrained by certain structural types or formations, although the exact number and definition of the latter remains a matter of debate (Theurillat et al. 1995; Dengler et al. 2005; Faber-Langendoen et al. 2014; Willner 2017). Thus, some authors proposed that the same species could be character species within two different formations or structural types (Dengler et al. 2005). However, formation-specific character species are in fact a special case of shared differential species rather than true character species. They should only be used if a species is similarly frequent and vital within two formations and therefore would not be suitable as character species of a single syntaxon. For instance, the dwarf-shrub *Erica carnea* grows with equally high constancy and cover

within dry pine forests and in treeless dwarf-shrub heaths of Central Europe. Thus, if pine forests and dwarf-shrub heaths are classified in different classes, *Erica carnea* could not be used as unique character species of any syntaxon. However, it might be accepted as formation-specific character species for both a pine-forest and a dwarf-shrub syntaxon. On the other hand, species that clearly have their optimum outside of forests and only occasionally occur under a tree canopy, or just as successional relics, should not be used as formation-specific character species of forest syntaxa, as they could not survive in the absence of their true, treeless habitat. Alliances solely based on formation-specific character species should be avoided unless there is no other reasonable solution.

Another issue that needs further attention is the frequency of the character species within the alliance. Since alliances are usually not only defined by character but also by differential species, the absence of character species in some associations is not a problem. However, is a single character species with restricted geographical range and very low constancy sufficient to raise a vegetation unit to alliance rank? Without putting forward precise threshold values, I suggest as a minimum requirement that at least one character species of the alliance should either occur in most associations with low (<20%) to moderate (20–60%) constancy or in some associations with high (>60%) constancy. Transgressive character species of associations are, by definition, character species of the alliance (Westhoff and van der Maarel 1978; Dengler et al. 2005). In any case, the alliance is not necessarily the lowest syntaxon that has a character species.

The biogeographical meaning of higher syntaxa

The proposed alliance concept emphasises the importance of intensive floristic definitions of higher syntaxa (De Cáceres et al. 2015), and the special role of character species for these definitions. As already indicated by Braun (1915), vegetation units based on coherent groups of character species are more than arbitrary boxes of similar plant communities. The one-to-one relationship between character species and vegetation units gives the latter a clear biogeographical and even evolutionary meaning. Associations, in contrast, often lack true character species. They are temporally less stable, especially in regions strongly affected by the climatic fluctuations of the Pleistocene. Therefore, from a global perspective, alliances could be perceived as more fundamental units than the associations, although the latter are formally the basic units of the phytosociological system. However, there are cases that may differ, such as vegetation types characterised by highly competitive, often monodominant species (e.g. marsh vegetation). In such vegetation, associations are mostly defined by the dominance of a single transgressive species, and the alliances by the frequent co-occurrence of these species as well as by differential species from other classes, while specific alliance species are lacking (Landucci et al. 2020). In these cases, the associations might be regarded as more fundamental than the alliances.

Syntaxa are abstract units, but the patterns behind them are real. Well-supported groups of character species (i.e., frequently co-occurring species with similar habitat requirements and similar geographical ranges) could be interpreted, to some degree, as natural entities reflecting a common biogeographical history of the species. However, despite the recent advances in phylogenetics and historical biogeography, the evolution of higher syntaxa has gained little attention in the scientific literature (but see Deil 1999, 2014 for some attempts in this direction). There are four possible mechanisms of "syntaxon evolution", which in most cases will act simultaneously: (i) speciation, (ii) extinction, (iii) adaptation of species to new habitats, and (iv) species migration (see Wiens 2012 for a similar model). For instance, isolation over long time periods might result in a previously wide-spread syntaxon being split into two or more syntaxa, each with its own set of character species. Alternatively, new habitats or areas might become available which are colonised by existing species. This colonisation might be accompanied by evolutional changes, leading to new species or subspecies, which subsequently become character taxa of new syntaxa (Figure 1). The alpine plant radiation, triggered by the uplift of high mountain systems during the late Tertiary (Hughes and Atchison 2015), has probably given rise to the numerous classes and orders of high-mountain vegetation described from Europe and other continents. Alliances might rather reflect the migration, extinction and speciation events caused by the climatic oscillations of the Pleistocene (Comes and

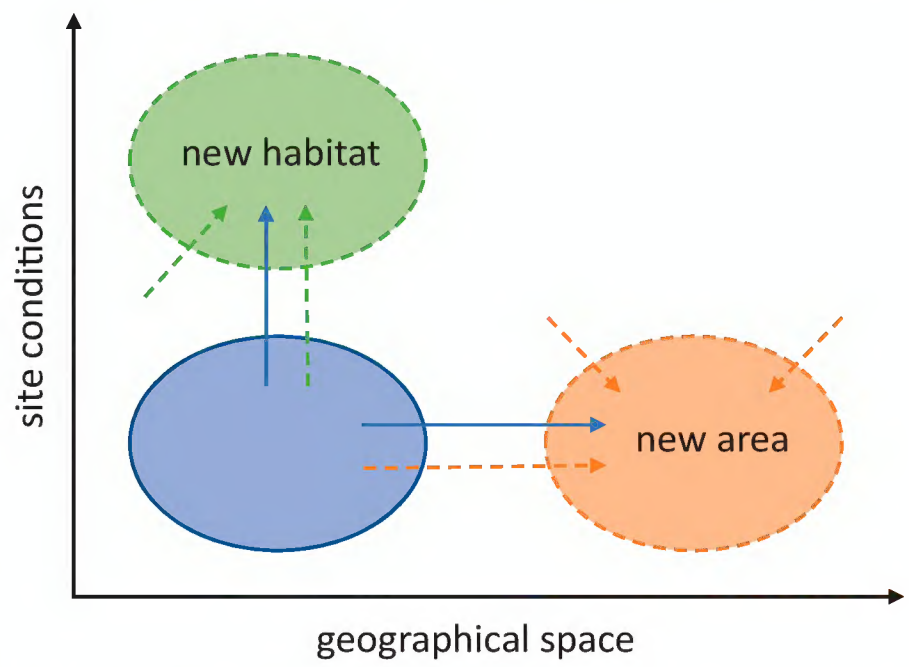

Figure 1. Two simple scenarios for the emergence of new syntaxa. Blue circle: old syntaxon. Green and orange circles: newly emerging syntaxa. Solid blue arrows: species colonising and adapting to a new habitat or area. Dashed arrows: colonisation coupled with evolutionary changes, leading to new species or subspecies, which become character taxa of the new syntaxa.

Kadereit 1998; Willner et al. 2009, 2017). Adaptation to a new habitat might shift the ecological niche of a species in such way that its optimum lies no longer in its original but in a new syntaxon. For instance, *Arrhenatherum elatius*, now the main character species of nutrient-rich mesic grasslands of Europe and almost exclusively found in anthropogenic habitats, is thought to have originated from nutrient-rich scree communities (Ellenberg 2009). Thus, a syntaxon can be much younger than its character species, but obviously it cannot be older. It is safe to assume that the age of alliances, orders and classes varies from a few hundred years in case of some types of anthropogenic vegetation to millions of years in case of old natural habitats.

Conclusions and outlook

Braun-Blanquet's original association concept provides a promising basis for defining the alliance. Otherwise, any grouping of associations could become an alliance, and the "inflation of higher syntaxa" (Pignatti 1995) could go on forever. However, there is more than just a practical need for this concept. The one-to-one relationship between character species and higher syntaxa offers the opportunity for integrating phytosociology and biogeographical-evolutionary studies, a scientific field that has hardly been explored.

The EuroVegChecklist (Mucina et al. 2016) was accompanied by expert-derived diagnostic species lists for the classes. The task of evaluating these species lists using large plot data sets and identifying the diagnostic species for the alliances and orders is still in the early stages. Optimally, this should be done with a simultaneous revision of the syntaxonomic system. The alliance concept outlined in this paper could serve as a helpful tool for these exercises.

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Supplementary material

Supplementary material 1
Associations in Braun (1915) and corresponding syntaxa in the EuroVegChecklist (Mucina et al. 2016).
Link: https://doi.org/10.3897/VCS/2020/56372.suppl1